DOES VEGETATION STRUCTURE LIMIT THE DISTRIBUTION OF NORTHERN GOSHAWKS IN THE OREGON COAST RANGES?

STEPHEN DESTEFANO¹

National Biological Service, Oregon Cooperative Wildlife Research Unit, 104 Nash Hall, Oregon State University, Corvallis, OR 97331 U.S.A.

JON MCCLOSKEY²

Bureau of Land Management, Salem District Office, 1717 Fabry Road, Salem, OR 97306

ABSTRACT.—Northern Goshawks (*Accipiter gentilis*) breed in a variety of forested areas throughout the Pacific Northwest. Nevertheless, they were only first found breeding in the Coast Ranges of Oregon in 1995, despite apparently suitable habitat and abundant prey. We document the rarity of goshawks in the Coast Ranges by reviewing previous and current survey results for nests of goshawks and other forest birds since the 1960s, examining sightings of goshawks since 1980 and reporting on a survey we conducted in 1994. We suggest that nesting goshawks are rare in the Coast Ranges because of the vegetative structure of the area and its influence on prey availability.

KEY WORDS: Northern Goshawk; Accipiter gentilis; distribution; habitat; foraging; reproduction; Oregon.

Puede ser que la estructura de vegetación limite la distribución de Accipiter gentilis en la sierra costa de Oregon.

RESUMEN.—Accipiter gentilis se crían en una variedad de áreas de bosque en todas partes del noroeste pacifico. Sin embargo, la primera vez que los encontraron en la sierra costa de Oregon fue en 1955, a pesar de suficiente hábitat conveniente y presa abundante. Nosotros documentamos la rareza de A. gentilis en la sierra costa examinando anterior y corriente resultados de estudios para nidos de A. gentilis y otros pájaros de bosque desde los 1960s, examinando observaciones de A. gentilis desde 1980 y reportando un estudio que nosotros conducimos en 1994. Nosotros pensamos que los A. gentilis que hacen nido en la sierra costa es raro por la estructura de vegetación en el área y su influencia en la disponibilidad de presa.

[Traducción de Raúl De La Garza, Jr.]

Northern Goshawks (Accipiter gentilis) are distributed across northern North America and throughout forested areas of the western U.S. (Palmer 1988). They nest in a variety of forest types, including boreal, deciduous and western coniferous forests. In Oregon, goshawk nests are found throughout forested areas east of the Cascade Mountain Range, on east and west slopes of the Cascade Range, in the Siskiyou Mountains of southwestern Oregon and even in isolated stands of aspen (*Populus* spp.) in mountain draws and valleys in the

Great Basin region of southeastern Oregon (Marshall 1992). Goshawks were not known to breed in the Coast Ranges of western Oregon, even though their nests are found in all other areas of the state (Reynolds et al. 1982, Marshall 1992). Incidental sightings of goshawks have been reported in the Coast Ranges, but it was not until 1995 that two pairs of goshawks were found breeding there (Thrailkill and Andrews 1996).

Reynolds (1975, 1978) found breeding pairs of Cooper's Hawks (*Accipiter cooperii*) and Sharpshinned Hawks (*A. striatus*), but not goshawks after an extensive search of the Coast Ranges from 1968–78. He speculated that forest conditions, specifically dense understories which may interfere with a goshawk's ability to hunt, precluded goshawks from breeding in this area (Reynolds and

¹ Present address: USGS, Arizona Cooperative Fish and Wildlife Research Unit, 104 Biological Sciences East, University of Arizona, Tuscon AZ 85721.

² Present Address: Winema National Forest, 38500 Highway 97 N, Chiloquin, OR 97624.

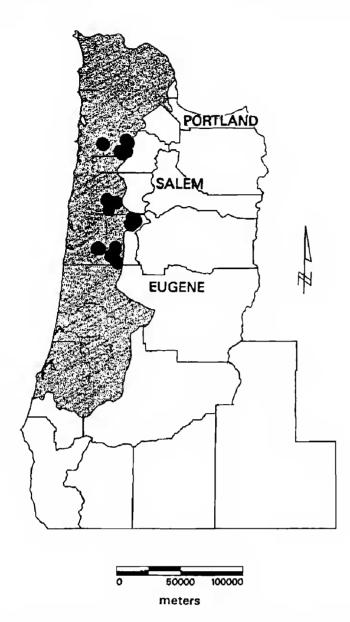


Figure 1. The Coast Ranges (shaded area) of western Oregon and areas (circles, which may represent ≥ 1 survey blocks) surveyed for Northern Goshawks during June-August 1994.

Wight 1978, Reynolds et al. 1982). No one has conducted systematic searches for goshawk nests in the Coast Ranges since, and no one has used broadcasts of goshawk vocalizations to survey for the presence of breeding pairs over large areas of the Coast Ranges (Woodbridge, USDA Forest Serv. unpubl. rep. 1990; Kennedy and Stahlecker 1993). Herein, we report results of a study conducted to document the presence of breeding Northern Goshawks and to assess vegetative conditions that might influence their distribution in the Oregon Coast Ranges.

STUDY AREA

The Coast Ranges of western Oregon lie north of the Coquille River and west of the Willamette Valley, and are separate from the Siskiyou Mountains in the southwestern corner of Oregon (Fig. 1). Topography is steep and dissected by many streams. Elevations range from sea level to 450–750 m at main ridge summits, with scattered peaks as high as 1250 m. Climate is characterized by mild, wet winters and relatively dry summers (Franklin and Dyrness 1973).

Historically, the Coast Ranges were densely forested with sitka spruce (*Picea sitchensis*), western hemlock (*Tsu*ga heterophylla) and western redcedar (Thuja plicata) (Franklin and Dyrness 1973). Most of the mature forest (>80 yr old) has been logged or burned during the past 150 yr (Franklin and Dyrness 1973). Much of what remains are stands of second-growth trees with older stands occurring as islands, fragmented by clearcut logging. As a result of these disturbances, and because of tree planting, Douglas-fir (*Pseudotsuga menziesii*) is now the major component of the forests in this area. Western hemlock and western redcedar are common coniferous species and red alder (Alnus rubra), vine maple (Acer circinatum) and bigleaf maple (A. macrophyllum) are common hardwood species (Franklin and Dyrness 1973, Forsman et al. 1996b).

Methods

Goshawk Surveys. We surveyed for Northern Goshawks in 24 survey blocks, totaling 3285 ha (range 60-335 ha) during June-August 1994. Surveys covered the east and west slopes of the Coast Ranges and included federally administered public lands, the MacDonald-Dunn State Forest managed by Oregon State University and areas originally searched by Reynolds (1975, 1978). To maximize the potential for locating nesting goshawks, survey blocks were chosen based on our knowledge of goshawk nesting habitats (DeStefano et al. 1994), past sightings of goshawks, recommendations from agency biologists familiar with local conditions and habitat and examination of aerial photographs and topographic maps to determine accessibility of potential goshawk habitat. Whenever possible, older (>80 yr), larger contiguous forested blocks were surveyed. Because we were more interested in documenting the presence of breeding goshawks rather than calculating an unbiased estimate of nesting density, we focused on areas with the greatest potential for nesting habitat, based on the published literature and our experience in Oregon. We did, however, survey a variety of forest types and seral stages.

We used taped vocalizations of Northern Goshawks to elicit responses from adults and juveniles (Woodbridge, USDA Forest Serv., unpubl. rep. 1990; Kennedy and Stahlecker 1993); the adult alarm call was used during the nesting period in June-July, and both adult alarm and juvenile begging calls were used during the post-fledging period in July-August. Road and foot transects were first delineated on maps and aerial photographs. Foot transects were 200 m apart with broadcast stations every 300 m; stations along adjacent transects were staggered (Joy et al. 1994). Broadcast stations on roads were 250 m apart. At each station, vocalizations were broadcast in three directions (60°, 180°, and 300°) for 10 sec, with 30 sec between each call. This procedure was conducted at each station by one or two observers. Presence, location and behavior of raptors were recorded.

Historical Sightings. To document past sightings of goshawks in the Coast Ranges, we searched records and data bases compiled from 1980–1995 by state and federal land management and conservation agencies and local birdwatchers. We assessed the reliability of these sightings and categorized them as 1 (questionable = observer had no or little experience identifying birds, or experience could not be assessed), 2 (reliable = experienced birder) and 3 (confirmed = experience observing raptors, professional biologist). Records were searched for date observed, behavior of adults, presence of immatures and other clues that might indicate reproductive activity. We also questioned biologists who have been conducting extensive surveys for Northern Spotted Owls (*Strix occidentahs*) and Marbled Murrelets (*Brachyramphus mamoratus*) in the Coast Ranges for the past 10–15 yr (see Nelson and Sealy 1995 and Forsman et al. 1996a for background and methods).

Vegetation Surveys. We examined vegetation in the 24 survey blocks for forest stand structure and composition, understory conditions and landscape patterns. Stand canopy structure, % canopy cover and tree species were recorded from ground surveys and aerial photos. After conducting ground assessments at each survey block, we then used a Geographic Information System (GIS) to calculate % cover of forest type and amounts of mature (>80 yr) and second-growth forest in survey blocks. We recorded the presence and % cover of dominant understory plant species at each survey site. Understory vegetation was classified into six associations, according to Franklin and Dyrness (1973), and represented a gradient from dry to wet conditions. These associations were (1)ocean-spray-salal (Holodiscus discolor-Gaultheria shallon) association found in dry, relatively open sites, (2) Pacific rhododendron-Oregon grape (Rhododendron macrophyllum-Berberis nervosa) found on dry, exposed ridgetops, (3) big huckleberry-beargrass (Vaccinium membranaceum-Xerophyllum tenax) on shallow, stony soils at high elevations, (4) vine maple-salal in cool, moist sites with moderately dense tree cover, (5) swordfern (Polystichum munitum) in moist sites associated with mature overstory conditions, and (6) swordfern-Oregon oxalis (Oxalis oregana) along streamside slopes.

RESULTS

Goshawk Surveys. We found no Northern Goshawks in the entire 3285 ha survey area. However, we did find two Sharp-shinned Hawks, seven Redtailed Hawks (*Buteo jamaicensis*) and two unidentified raptors (too small to be goshawks). We also found two small, unoccupied accipiter nests (probably Sharp-shinned Hawks built in previous years).

Vegetation Surveys. Of the 24 survey blocks covered, 23 were dominated by a Douglas-fir overstory. The one remaining block was a fire-regenerated stand dominated by noble fir (*Abies procera*); this site was undisturbed by logging, except for access roads. For all 24 survey blocks combined, 63% of the area was in older (>80 yr) Douglas-fir with 85% canopy cover, 24% was conifer-hardwood mix (Douglas-fir, western hemlock, western redcedar, red alder, vine and bigleaf maple) with $\leq 65\%$ canopy cover, 7% was open mixed conifer (Douglasfir, western hemlock, western red cedar) with \geq 65% canopy cover, 3% was young (<80 yr) Douglas-fir with \geq 85% canopy cover, 2% was older Douglas-fir with \leq 30% canopy cover, and 1% was clearcut areas, meadows or water.

Ground cover within the survey blocks was dominated by understory types 4 and 5; these two types were present in 20 and 14 of the 24 stands, respectively. Vine maple, salal and swordfern were the most common species overall, and each survey block, with the exception of the stand of noble fir, had a dense shrub layer with 45–100% ground cover ($\bar{x} = 81\%$, SE = 3%, N = 23). Twenty-three of the 24 blocks were previously disturbed by logging and fire.

Historical Sightings. Records of previous sightings indicated that goshawks have been seen throughout the Coast Ranges every year, and during each month in any given year, for the past 15 years (Table 1), with apparent peaks in sightings in the spring and fall (Fig. 2). This would coincide with dispersing or migrating hawks. Numbers of observations were low, however, and prior to 1995, no confirmed evidence of reproductive activity had been documented. Few reports have described aggressive, territorial behavior or repeated sightings of adults in a particular area during the breeding season. Goshawk sightings in the Coast Ranges have been much lower than for other parts of the state (Fig. 3).

DISCUSSION

Determining the "absence" or rarity of a species in a geographic region, and whether or not this is meaningful ecologically, can be a difficult task, especially when the species is normally secretive and present in low densities. At least two elements are involved in making this determination. The first is that large-scale searches (both spatially and temporally) must be conducted because occupation of habitat by a species can vary over space and time (Morris 1987, Block and Brennan 1993, DeStefano et al. 1994, Keane and Morrison 1994). Our survey for goshawks over a single breeding season is obviously inadequate to address this concern, but coupled with surveys in the 1960s and 1970s, the consistent and widespread searches for Northern Spotted Owl and Marbled Murrelet nests during the 1970s-90s, and the reports of birdwatchers and agency biologists for the past 15 years, the temporal and spatial scope of the search for goshawk nests in the Coast Ranges has been broad.

The second element involves a determination,

	Age				
YEAR	Adult	Імм.	Unk.	Observed Behaviors	Source ^a
1995	4	5	0	2 nests located on BLM lands	BLM, OCWRU
1994	3	1	5	Hunting, calling, respond to owl tape, fly-by	Private, OCWRU, BLM
1993	1	0	5	Unknown	OB 19:57, BLM, ONHP, Private
1992	3	1	2	Fly-by, perched, soaring, unknown	OCWRU, BLM, Private
1991	0	0	2	Unknown	BLM, Private
1990	3	0	5	Near spotted owl nest, chasing spotted owl, unknown	OB 16:94,185, BLM, Private
1989	1	0	1	Fly-by, unknown	BLM, Private
1988	1	1	2	Unknown, soaring	Private
1987	1	2	2	Unknown, aggressive interaction with red-tailed hawk	OB 13:232,314, Private, Crannel and DeStefano 1992
1986	0	0	2	Unknown	OB 12:212
1985	0	0	6	Unknown	USFS, Private
1984	1	2	1	Unknown, soaring	Private
1983	0	0	2	Unknown	OB 10:130, Private
1982	0	0	4	Unknown	Private
1981	0	0	4	Unknown	Private
1980	0	0	2	Unknown	Private

Table 1. Sightings of Northern Goshawks, grouped by year, in the Coast Ranges of western Oregon, 1980–95. Only records by experienced agency biologists or birders (levels 2 and 3; see text) were used. Unknown age or behavior indicates observer was unsure or information was not reported.

^a Source codes: BLM = Bureau of Land Management; OB = various issues (vol.:page) of the journal Oregon Birds (individual issues not listed in Lit. Cited); OCWRU = Oregon Cooperative Wildlife Research Unit; ONHP = Oregon Natural Heritage Program; Private = records of private individuals; USFS = U.S. Forest Service.

probably on both objective and subjective bases, that a species is absent from a region because important components of the habitat are lacking. Otherwise, the absence of a species from a region is meaningless. Our contention is that the absence, or at least rarity, of nesting goshawks in the Coast Ranges of western Oregon is an interesting phe-

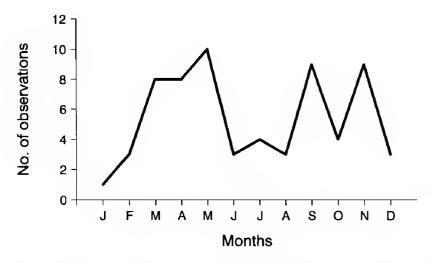


Figure 2. Distribution of Northern Goshawk sightings by month, consolidated for the years 1980–95, in the Coast Ranges of western Oregon. Adults and young from two nest sites located in June 1995 are not included.

nomenon, and one that suggests something about vegetation structure on the distribution of this species.

The Northern Goshawk has been called a forest habitat generalist (Reynolds et al. 1992). The location of the Coast Ranges of western Oregon in relation to the geographic range of the goshawk in North America, and the general forest conditions (mixture of mature and second-growth coniferous forest and openings) that exist there, appear to indicate that the Coast Ranges should be part of the breeding range of this species. Rarity is common along the geographic boundaries of a species' range, yet goshawks nest in areas north, south, and east of the Coast Ranges.

Why is there a gap in the breeding range of this species and what is it about the Coast Ranges of Oregon that prevents goshawks from nesting there? It could be related to climate. The Coast Ranges receive 150–300 cm of annual rainfall (Franklin and Dryness 1973), much of it falling during the spring breeding season. However, Northern Goshawks breed commonly on the



Figure 3. Relative abundance of Northern Goshawks by county in Oregon, based on records of the Oregon Audubon Society and Oregon Department of Fish and Wildlife. Abundance ratings are common (black), occasional (dark gray), rare (light gray), and unknown (white). Note that coastal regions of Lane and Douglas Counties would likely be rated as having rare (light gray) sightings of goshawks, but both counties are rated as occasional (dark gray) because large portions of each reach into the Cascade Mountain foothills and range, where goshawks are seen more often.

Olympic Peninsula of Washington (E. Forsman pers. comm.) and in southeastern Alaska (K. Titus pers. comm.), where annual precipitation equals or exceeds levels received in Oregon's Coast Ranges.

A second possibility might involve predation or competition from other raptors. Great Horned Owls (*Bubo virginianus*) and Red-tailed Hawks frequently interact with Northern Goshawks and often use their nests (Moore and Henny 1983, Crannell and DeStefano 1992, Rohner and Doyle 1992). It is unlikely, though, that this form of predation and/or competition is more intense in the Coast Ranges than other parts of the goshawks' geographic range.

The third explanation involves vegetation structure as it relates to prey availability. Goshawks tend to hunt in the ground-shrub and shrub-canopy zones of the forest (Reynolds and Meslow 1984). A dense shrub layer is characteristic of most forest areas of the Coast Ranges and disturbances such as logging and fire have decreased mature overstory canopy closure, allowing more sunlight to reach the ground. These conditions, coupled with high levels of rainfall, have resulted in increased understory stem densities and dense, lush undergrowth on many sites (Franklin and Dyrness 1973). Prey, which are varied and abundant in the Coast Ranges, include such species as snowshoe hares (Lepus americanus), brush rabbits (Sylvilagus bachmani), Douglas squirrels (Tamiasciurus douglasii), Ruffed Grouse (Bonasa umbellus), Mountain Quail (Oreortyx pictus), Northern Flickers (Colaptes auratus) and other woodpeckers, and Stellar's and Gray Jays (Cyanocitta stellari and Perisoreus canadensis, respectively). Many of these prey species may be difficult for goshawks to capture because of the dense understory conditions that exist throughout most of the Coast Ranges (Reynolds and Meslow 1984). In addition, the larger biomass prey species (lagomorphs, grouse) may be more important to breeding goshawks than smaller prey (jays, woodpeckers) (Reynolds et al. 1992), and low availability of larger prey may depress reproductive potential (Alaska Dept. Fish and Game 1993). Dense understory conditions would make the larger, grounddwelling species more difficult to capture (Reynolds et al. 1992).

Others have found the distribution of raptor foraging to be inversely related to the density of plant cover (Southern and Lowe 1968, Wakely 1978, Baker and Brooks 1981, Bechard 1982, Collopy and Bildstein 1987). Preston (1990) summarized these findings by describing raptor hunting distribution as a function of both prey abundance and availability, which in turn is a function of a suite of environmental factors, including habitat characteristics (e.g., vegetation structure). In fact, suitable foraging habitat may be more important than nesting habitat in determining the distribution of goshawks in boreal forest (Widén 1989). The importance of prey in the distribution and management of northern goshawks has been emphasized in the management guidelines of Reynolds et al. (1992).

If a relationship between vegetation structure and availability of prey does indeed exist, then the forest conditions present in the Coast Ranges of Oregon may limit prey availability to goshawks and thus prevent or depress reproductive activity, despite potentially suitable nesting substrate and adequate populations of prey.

ACKNOWLEDGMENTS

We thank W. Dean, D.S. Hopkins and J.A. Reid (Bureau of Land Management), E.D. Forsman and S.J. Madsen (U.S. Forest Service), C. Bruce and T. O'Neil (Oregon Department of Fish and Wildlife), M. Hansen, S.K. Nelson, J.A. Thrailkill, and M. Wilson (Oregon Cooper-

39

ative Wildlife Research Unit), and E. Schauber and S. Spean (Oregon State University) for providing field support and/or information on goshawk sightings. Special thanks to R. Bayer, E. Eltzroth, D. Faxon, G. Gilson, T. Mickel and H. Nehls for sharing their private records. The manuscript benefited from reviews by P. Beier, S.K. Daw, S.M. Desimone, E.D. Forsman, M.T. McGrath, M.L. Morrison and R.T. Reynolds. Additional logistical support was provided by the Oregon Cooperative Wildlife Research Unit and the Department of Fisheries and Wildlife at Oregon State University.

LITERATURE CITED

- ALASKA DEPARTMENT OF FISH AND GAME. 1993. A summary of survey, radio-telemetry, and other results regarding goshawk field studies in southeast Alaska. Alaska Dep. of Fish and Game, Juneau, AK U.S.A.
- BAKER, J.A. AND R.J. BROOKS. 1981. Distribution patterns of raptors in relation to density of voles. *Condor* 83: 42-47.
- BECHARD, M.J. 1982. Effect of vegetative cover on foraging site selection by Swainson's Hawks. *Condor* 84: 153–159.
- BLOCK, W.M. AND L.A. BRENNAN. 1993. The habitat concept in ornithology: theory and applications. *Current Ornithol.* 11:35–91.
- COLLOPY, M.W. AND K.L. BILDSTEIN. 1987. Foraging behavior of Northern Harriers wintering in southeastern salt and freshwater marshes. *Auk* 104:11–16.
- CRANNELL, D. AND S. DESTEFANO. 1992. An aggressive interaction between a Northern Goshawk and a Redtailed Hawk. J. Raptor Res. 26:269–270.
- DESTEFANO, S., S.K. DAW, S.M. DESIMONE AND E.C. MES-LOW. 1994. Density and productivity of Northern Goshawks: implications for monitoring and management. *Studies in Avian Biol.* 16:88–91.
- FORSMAN, E.D., S. DESTEFANO, M.G. RAPHAEL AND R.J. GUTIÉRREZ, [EDS.]. 1996a. Demography of the Northern Spotted Owl. *Studies in Avian Biol.* 17.
 - —, P.J. LOSCHL, R.K. FORSON AND D.K. BARRETT. 1996b. Demography of Northern Spotted Owls on the Siuslaw National Forest, Oregon. *Studies in Avian Biol.* 17:47–52.
- FRANKLIN, J.F. AND C.T. DYRNESS. 1973. Natural vegetation of Oregon and Washington. USDA Forest Service, Gen. Tech. Rep. PNW-8, Portland, OR U.S.A.
- JOY, S. M., R.T. REYNOLDS AND D.G. LESLIE. 1994. Northern Goshawk broadcast surveys: hawk response variables and survey cost. *Studies in Avian Biol.* 16:24–30.
- KEANE, J.J. AND M.L. MORRISON. 1994. Northern Goshawk ecology: effects of scale and levels of biological organization. *Studies in Avian Biol.* 16:3–11.
- KENNEDY, P.L. AND D.W. STAHLECKER. 1993. Responsiveness of nesting Northern Goshawks to taped broad-

casts of 3 conspecific calls. J. Wildl. Manage. 57:249-257.

- MARSHALL, D.B. 1992. Status of the Northern Goshawk in Oregon and Washington. Audubon Society of Portland, Portland, OR U.S.A.
- MOORE, K.R. AND C.J. HENNY. 1983. Nest site characteristics of three coexisting accipiter hawks in northeastern Oregon. *Raptor Res.* 17:65–76.
- MORRIS, D.W. 1987. Ecological scale and habitat use. *Ecology* 68:362-369.
- NELSON, S.K. AND S.G. SEALY, [EDS.]. 1995. Biology of the Marbled Murrelet: inland and at sea. Northwest. Nat. 76.
- PALMER, R.S. 1988. Handbook of North American birds. Vol. 4. Yale Univ. Press, New Haven, CT U.S.A.
- PRESTON, C.R. 1990. Distribution of raptor foraging in relation to prey biomass and habitat structure. *Condor* 92:107–112.
- REYNOLDS, R.T. 1975. Distribution, density, and productivity of three species of accipiter hawks in Oregon. M.S. thesis, Oregon State Univ., Corvallis, OR U.S A.
- ——. 1978. Food and habitat partitioning in two groups of coexisting *Accipiter*. Ph.D. dissertation, Oregon State Univ., Corvallis, OR U.S.A.
- ——, R.T. GRAHAM, M.H. REISER, R.L. BASSETT, P.L. KENNEDY, D.A. BOYCE, JR., G. GOODWIN, R. SMITH AND E.L. FISHER. 1992. Management recommendations for the Northern Goshawk in the southwestern United States. USDA Forest Serv., Gen. Tech. Rep. RM-217, Fort Collins, CO U.S.A.
- ——, AND E.C. MESLOW. 1984. Partitioning of food and niche characteristics of coexisting Accipiter during breeding. Auk 101:761–779.
- ——, E.C. MESLOW AND H.M. WIGHT. 1982. Nesting habitat of co-existing *Accipiter* in Oregon. J. Wildl. Manage. 46:124–138.
- —, AND H.M. WIGHT. 1978. Distribution, density, and productivity of accipiter hawks breeding in Oregon. *Wilson Bull*. 90:182–196.
- ROHNER, C. AND F.I. DOYLE. 1992. Food-stressed Great Horned Owl kills adult goshawk: exceptional observation or community process? *J. Raptor Res.* 26:261– 263.
- SOUTHERN, H.N. AND V.P.W. LOWE. 1968. The pattern of distribution of prey and predation in Tawny Owl territories. J. Anim. Ecol. 37:75–97.
- THRAILKILL, J.A. AND L.S. ANDREWS. 1996. Presence of breeding Northern Goshawks in the Coast Ranges of Oregon. J. Raptor Res. 30:248–249.
- WAKELY, J.S. 1978. Factors affecting the use of hunting sites by Ferruginous Hawks. *Condor* 80:316–326.
- WIDÉN, P. 1989. The hunting habitats of goshawks Accepiter gentilis in boreal forests of central Sweden. Ibis 131: 205–213.

Received 1 April 1996; accepted 23 November 1996